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Mantle display and glochidia release behaviors of five quadruline freshwater mussel species (Bivalvia: Unionidae)

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Abstract: Diverse strategies have evolved in freshwater mussels to promote the transfer of their parasitic larvae to host fish. Among these, modification of the mantle as a host attracting lure has been well-documented in the Tribe Lampsilini, but only recently reported in the Tribe Quadrulini. Here we describe mantle modifications and glochidia release behaviors in five quadruline species, including members of the *Quadrula quadrula* (Rafinesque, 1820), *Q. pustulosa* (Lea, 1831), and *Q. metanevra* (Rafinesque, 1820) species groups. Displays were motionless and consisted of inflated mantle tissue surrounding the excurrent aperture. Gross display morphology was largely variable among species: *Q. fragosa* (Conrad, 1835) and *Tritogonia verrucosa* (Rafinesque, 1820) had relatively large, uniquely shaped displays; *Cyclonaias tuberculata* (Rafinesque, 1820) and *Q. pustulosa* had smaller, stomate-shaped displays; and *Q. metanevra* had a diminutive, polyp-like display. *Cyclonaias tuberculata* exhibited a bimodal host infection strategy where individuals had either a mantle display or released a gelatinous conglutinate. *Quadrula pustulosa* and *Q. metanevra* expelled glochidia in a forceful burst when their displays were touched. Quadruline mantle displays do not clearly mimic identifiable aquatic organisms suggesting they may represent non-specific food items to their fish hosts.

Key words: fish lure, life history, *Quadrula*, *Cyclonaias*, *Tritogonia*

The freshwater bivalve family Unionidae is a group of mostly riverine mollusks that have their greatest diversity in eastern North America (Graf and Cummings 2007, Bogan 2008). Most unionids have a life cycle in which their larvae (glochidia) are obligate parasites on vertebrate hosts, usually attaching to the gills or fins of fish where they may undergo transformation into free-living juveniles (Kat 1984, Wächtler *et al.* 2001). Many species have evolved impressive strategies to facilitate transfer of glochidia to the host, usually involving some form of food mimicry. Well-known examples include: mantle modifications "lures or displays" that resemble fish or invertebrates (Barnhart and Roberts 1997, Haag *et al.* 1999, Haag and Warren 2003, Allen *et al.* 2007, Rypel 2008), packaging of glochidia into conglutinates resembling insects or worms (Barnhart and Roberts 1997, Watters 1999, Jones and Neves 2002, Haag and Warren 2003), and minnow-like superconglutinates (Haag *et al.* 1995, Hartfield and Butler 1997). In most cases, the morphology of these lures appear well-suited to the feeding habits of the host.

Multiple genera in the Tribe Lampsilini use mantle displays as a host attraction strategy (Zanatta and Murphy 2006, Barnhart *et al.* 2008); however, these structures were only recently recognized in the Tribe Quadrulini (Barnhart *et al.* 2008). In that study, *Quadrula cylindrica* (Say, 1817), *Q. fragosa* (Conrad, 1835), *Q. pustulosa* (Lea, 1831), and *Tritogonia verrucosa* (Rafinesque, 1820) were shown to have mantle displays (termed the mantle magazine), and some aspects of glochidia brooding and release behaviors were discussed. As currently recognized, the genus *Quadrula* Rafinesque, 1820 is composed of three distinct clades, the *quadrula*, *pustulosa*, and *metanevra* species groups (Simpson 1900, Frierson 1927, Serb *et al.* 2003). Host fishes vary among these groups, with the *quadrula* and *pustulosa* species groups using catfishes (Ictaluridae) (Howard 1914, Howells 1997, Hove *et al.* 2001, Haag and Warren 2003, Steingraeber *et al.* 2007) and the *metanevra* species group using minnows (Cyprinidae) (Yeager and Neves 1986, Yeager and Saylor 1995, Crownhart *et al.* 2006). Assuming that mantle displays in these unionids facilitate glochidia transfer to the host, their morphology and brooding behaviors should be adapted to attract these disparate host groups.

Furthermore, there has been renewed debate regarding the classification of some quadruline species, such as the proposed placement of *Tritogonia* Agassiz, 1852 within *Quadrula* (Serb *et al.* 2003). *Cyclonaias* Pilsbry in Ortmann and Walker, 1922 is presumed to be a valid monotypic genus (Graf and Cummings 2007, Williams *et al.* 2008, Watters *et al.* 2009), yet its phylogenetic placement is uncertain (Heard and Guckert 1970, Serb *et al.* 2003, Campbell *et al.* 2005). There is further disagreement whether the three species groups should be lumped within *Quadrula* (Serb *et al.* 2003, Williams *et al.* 2008) or treated as distinct genera (Graf and

Cummings 2007, Watters *et al.* 2009). A better understanding of mantle display morphology and glochidia brooding behaviors within the Quadrulini could be helpful in resolving these questions.

In this study, we add to previous work by describing gross structure and phenology of mantle displays and glochidia release behaviors of five quadruline species, including members of the three primary quadruline clades. Since mantle display and conglutinate morphology presumably evolved to facilitate transfer of mussel larvae to its host(s) (Barnhart *et al.* 2008), and these structures apparently are adapted to suit the feeding habits of the host fish, we discuss our findings in context of known host associations.

MATERIALS AND METHODS

We studied unionid brooding behaviors in the St. Croix River at Interstate State Park, Minnesota and Wisconsin, U.S.A. (45° 23′ 36″N, 92° 39′ 47″W) between April and September, from 2004 to 2008. This reach of the St. Croix holds a regionally diverse assemblage of over 30 unionid species (Hornbach 2001), many of which are locally or globally rare. Hornbach *et al.* (1996) provides general habitat and unionid assemblage characteristics of the study area. We searched for displaying unionids every 1–4 weeks as time and conditions allowed, mostly at night using hand-held underwater lights. Diel patterns of displaying behavior were not examined in this study (but see Hove *et al.* 2011). Water clarity (≈ 1 m visibility) was suitable to easily observe unionids *in situ*. Water depth varied during the study, and we used SCUBA when depth was > 0.6 m, and a mask and snorkel otherwise. When a displaying mussel was encountered, we recorded underwater digital photographs (with flash) or video, then examined the specimen to confirm its identification and released it. We did not measure display dimensions, but estimated relative size compared to shell dimensions from photographs and video. Displays were categorized as either fully or weakly inflated by observing multiple displays over several years during the brooding period. We did not count displaying individuals because of difficulty tracking the area covered by up to 5 persons at night.

To simulate a fish encounter and elicit the release of glochidia, we touched or tapped displays with a fingertip while recording video. We captured released glochidia with a fine mesh net or plastic bag when possible, or extracted glochidia from a subset of displaying females. We examined glochidia with a light microscope, and considered them viable if they had fully formed valves and snapped shut after adding table salt to the water (Zale and Neves 1982).

Mean daily water temperature for observation dates was obtained from USGS gauging station 05340500 at St. Croix Falls, Wisconsin, approximately 2.4 km upstream of our study area. Voucher specimens of each species from the study area, although usually not of the displaying individuals (because of their protected status), are held in the University of Minnesota James Ford Bell Museum of Natural History.

RESULTS

Representative displays for the five mussel species are shown in Fig. 1. Additional photographs showing variation among individuals or different viewing angle, and video footage of distinct glochidia release behaviors are posted online (http://mndnr.gov/mussels/quadrula).

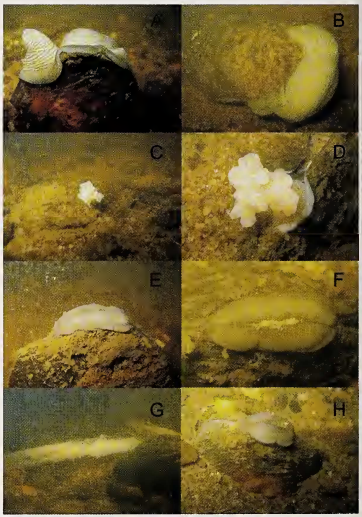

Figure 1. Typical quadruline mantle displays. **A**, *Quadrula fragosa* lateral view; **B**, *Tritogonia verrucosa* posterior-lateral view; **C**, *Quadrula metanevra* lateral view, and **D**, dorsal view close up; **E**, *Cyclonaias tuberculata*, lateral view; **F**, dorsal view close up, with glochidia clearly visible in the center of the display, and **G**, conglutinate, lateral view; **H**, *Quadrula pustulosa*, dorsal-lateral view; material in center of the display is sand.

Cyclonaias tuberculata

Display

Brooding female *Cyclonaias tuberculata* produced a relatively small, stomate-shaped display, by inflating the mantle region around the excurrent aperture (Figs. 1E–F). Displaying females emerged from the substrate such that approximately half of the posterior shell was exposed. Display length was about 35–40% of dorsal-ventral shell height, and the swollen mantle often enveloped a small portion of the posterior shell margin. Displays were bluish-grey with faint, dark speckles that frequently aligned to form horizontal lines. We observed displays from June to the beginning of August when daily water temperature ranged from 19 to 27 °C (Fig. 2), although within the brooding period individuals displayed for only about a month.

Glochidia release

Non-displaying *Cyclonaias tuberculata* released a gelatinous conglutinate that trailed from the excurrent aperture (Fig. 1G) and swayed with the water current (see video http://mndnr.gov/mussels/quadrula). Conglutinates were amorphous and transparent, varied in size from about 5 to 20 cm in length, and embedded glochidia were clearly visible. Some detached conglutinates were also observed lying on the substrate or tumbling on the stream bottom with the current. Conglutinates and mantle displays occurred at similar water temperatures and time of the year (Fig. 2), but these behaviors did not occur simultaneously within individuals. Some individuals had loosely assembled glochidia clearly visible between the swollen tissues of the mantle magazine (Fig. 1F). After several attempts, no displaying individuals expelled glochidia in response to the touch of a finger.

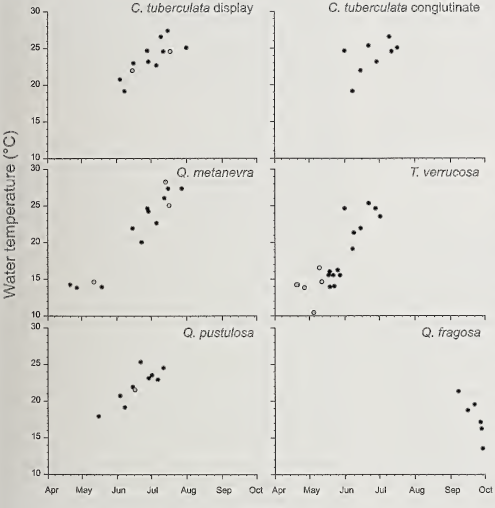

Figure 2. Phenology of displaying behavior for five quadruline mussel species in the St. Croix River, Minnesota and Wisconsin. Each point represents a date when one or more displaying individuals were observed. Black symbols are fully inflated displays; shaded symbols are weakly inflated displays (see text). *Cyclonaias tuberculata* conglutinate data include observations when a conglutinate was attached to the mussel or found detached. Water temperature data were retrieved online from the St. Croix Falls USGS gauging station 05340500 (http://waterdata.usgs.gov/wi/nwis/rt).

Quadrula fragosa

Display

Brooding female *Quadrula fragosa* had a large display that extended from the excurrent aperture to the posterior limit of the dorsal shell margin (Fig. 1A). Displaying females emerged from the substrate such that about 50–70% of the shell was exposed, and valves were oriented vertically with the anterior end remaining buried in the substrate. The most prominent feature of the display was a large conical knob-like structure with a rounded tip that formed the mantle magazine. This structure originated from mantle tissue next to the incurrent aperture, which was at the knob base. A slit, evidently composed of the excurrent aperture, ran from the tip of the knob until it connected with the incurrent aperture. Dorsal to the knob, the distended mantle formed broad wings that draped over the shell margin, with a v-shaped furrow at the midpoint where the wings joined. Relative size of displays varied among individuals. Displays were whitish to blue-grey, and the surface of the knob had well-defined

irregular horizontal stripes with interspersed speckles. Stippling on the wings formed fine striae, which were oriented perpendicular to the furrow. A few small tubercles occurred around the knob or in the furrow of three individuals. The display of two individuals appeared to be damaged. The wing margins were ragged and white, as if tissue had been torn away, and the knob tips were similarly discolored.

Female *Quadrula fragosa* displayed from mid to late September when daily water temperature ranged from 16.2 to 19.5 °C (Fig. 2).

Glochidia release

In the laboratory, a single *Quadrula fragosa* with a partially inflated display released conglutinates with mature glochidia, but the release was not a forceful expulsion (M. C. Hove pers. obs.). Conglutinates were thin and white, approximately 5 mm wide by 10 mm long, tapered at both ends, and fragmented somewhat easily but were not as fragile as *Tritogonia verrucosa* conglutinates. Because of the endangered status of this species, we touched the mantle display of just two specimens in the field and neither released glochidia. Additionally, on several occasions displaying animals touched the container walls during transport to the laboratory but did not release glochidia.

Quadrula metanevra (Rafinesque, 1820)

Display

The display of *Quadrula metanevra* was the smallest among the species studied and somewhat resembled a coral polyp (Figs. 1C–D). As the display developed, tissue surrounding the excurrent aperture inflated and became progressively wrinkled or folded, sometimes developing a short stalk at the base. The degree of wrinkling, which affected overall display shape, was variable among individuals. Relative display length was about 15–25% of dorsal-ventral shell height. Displays were usually whitish, occasionally light pink or light orange, with irregular faint mottling. Displaying females were oriented in the substrate similar to non-displaying individuals, being mostly or completely buried.

Quadrula metanevra displayed for about 3 months within a year, from mid-April to late July, when daily water temperature ranged from 13.9 to 24.6 °C (Fig. 2). This was the longest brooding period among species in this study.

Glochidia release

Five *Quadrula metanevra* expelled loose glochidia in forceful bursts when the displays were touched with a fingertip. Mature glochidia were captured from one such release. One individual released glochidia before it was touched, suggesting the observer nearby stimulated the release (see video http://mndnr.gov/mussels/quadrula).

Quadrula pustulosa

Display

Quadrula pustulosa's mantle display was very similar in appearance to *Cyclonaias tuberculata* (Fig. 1H). Relative display size varied among individuals, ranging between 30–50% of dorsal-ventral shell height. Color was light tan or grayish with faint or well-defined speckles that frequently aligned to form horizontal lines. Displaying females usually emerged from the substrate such that approximately 25 to 40% of the posterior shell was exposed. We observed displays for up to 2 months within a year, from mid-May to mid-July, when daily water temperature ranged from 17.9 to 25.3 °C (Fig. 2).

Glochidia release

Four *Quadrula pustulosa* expelled glochidia in forceful bursts when the displays were touched with a fingertip (see video http://mndnr.gov/mussels/quadrula). Glochidia were loose or weakly bound in a white material that readily fragmented, and was less cohesive than the gelatinous conglutinate produced by *Cyclonaias tuberculata*.

Tritogonia verrucosa

Display

Brooding *Tritogonia verrucosa* had a large fleshy display that extended around the entire curve of the posterior shell margin, from the dorsal-posterior point where the shell begins to slope, ventrally to where the posterior ridge meets the shell margin, and encompassed both the incurrent and excurrent apertures (Fig. 1B). Females emerged from the substrate in mid-April to early May, lying on their side or with the ventral margin down. After emergence, we observed displays in the early stages of development when average daily water temperature was < 13.5 °C. Fully inflated displays were seen between mid-May to early July, for 4.5 to 6.5 weeks within a brooding season, when daily water temperature ranged from 13.9 to 25.3 °C. The margin of the left and right mantle edges were finely serrated and frequently overlapped along the thickest region of the display. Displays were whitish, occasionally with varying degrees of bluish shading. The surface was covered with shallow, irregularly spaced, bluish or grey colored groves, lines, and pits, which gave displays a coarse or corrugated appearance. These characters, as well as display size, were variable among individuals. *Tritogonia verrucosa* was the most commonly observed displaying quadruline at our study site, and there were noticeable within-year peaks of displaying frequency indicating synchronous behavior.

Glochidia release

Tritogonia verrucosa released loose glochidia or broken and whole conglutinates but did not forcefully expel glochidia

in response to touch. Broken and whole conglutinates had an elongate rectangular outline, were 3 to 25 mm long and 2 to 3 mm wide, light yellow to light brown, and fragmented easily.

DISCUSSION

Display morphology and host associations

Host attraction strategies used by unionids generally involve one of two types of food mimicry, mantle modifications intended to lure host fish to the brooding mussel (Barnhart and Roberts 1997, Haag *et al.* 1999, Allen *et al.* 2007, Rypel 2008) or the release of conglutinates that resemble host food items (Haag *et al.* 1995, Barnhart and Roberts 1997, Hartfield and Butler 1997, Watters 1999, Jones and Neves 2002, Haag and Warren 2003). These features presumably evolved to suit the feeding habits of the host or a suite of host species, and are adapted to attract and facilitate glochidia transfer to the host (Zanatta and Murphy 2006). The hypothesis that quadruline mantle displays function as host-attracting lures is supported by the presence of mature glochidia in these individuals.

Size and shape of quadruline mantle displays varied among most species in our study; however, all were composed of inflated mantle tissue surrounding the excurrent aperture (as well as the incurrent aperture in *Tritogonia verrucosa*). This differs from described lampsiline mantle displays which are positioned anterior to the incurrent aperture along the ventral or posterior-ventral shell margin (Kraemer 1970, Haag *et al.* 1999, Allen *et al.* 2007). While their function in attracting host fish is likely similar, the distinct position of mantle displays in the Lampsilini and Quadrulini and the observation that these taxa are not sister lineages (Campbell *et al.* 2005) indicates that mantle displays evolved independently in these two clades.

We suspect that variation in display morphology among quadruline species is suited to the host fish, but it is unclear what food items are being mimicked. In our study area, channel catfish (*Ictalurus punctatus*) is likely the principal host for *Cyclonaias tuberculata*, *Quadrula fragosa*, and *Q. pustulosa* (Howard 1914, Hove 1997, Hove *et al.* 2001, Steingraeber *et al.* 2007) and flathead catfish (*Pylodictis olivaris*) for *Tritogonia verrucosa* (Howells 1997, Hove *et al.* 2011). Various minnows (Cyprinidae) are suitable hosts for *Q. metanevra* (Crownhart *et al.* 2006) and other species within the *metanevra* species group (Yeager and Neves 1986, Yeager and Saylor 1995).

In species with catfish hosts, pale color and absence of active movement indicate these lures might mimic dead or moribund fish, or perhaps live, moribund, or dead unionids. Channel and blue catfish (*Ictalurus furcatus*) will consume unionids, fingernail clams, and snails (Forbes 1888, Brown and Dendy 1961, Lewis 1976, Griswold and Tubb 1977), possibly in abundance (reviewed by Graham 1999), but they are not known to eat mature quadruline mussels. It is also possible these lures do not visually mimic a particular food item because selection on lure morphology has not been as strong with these species. Channel and blue catfish are omnivores, consuming a variety of food items including live fish (Bailey and Harrison 1948, Griswold and Tubb 1977, Pflieger 1997, Graham 1999, Edds *et al.* 2005), whereas flathead catfish primarily consume live prey: invertebrates when young and then turning piscivorous (Brown and Dendy 1961, Layher and Boles 1980, Pflieger 1997). Therefore, quadruline displays could simply represent a generalization of a subset of the many available food items these catfish consume, including live prey. Catfish also use taste and olfactory receptors to find food (Caprio 1978) so there could be a chemical signal associated with these lures (Barnhart *et al.* 2008, Hove *et al.* 2011), a hypothesis that remains to be tested. Although we did not record any fish-display interactions, Barnhart *et al.* (2008) observed channel catfish attack the display of *Tritogonia verrucosa*, even though this fish species is not a suitable host based on testing done by Hove *et al.* (2011). We encountered two seemingly damaged *Quadrula fragosa* displays which could have resulted from fish attacks.

Orientation of displaying females varied among species. Species that use catfish as hosts emerged from the substrate to varying degrees, and therefore, do not conceal themselves while brooding glochidia, a behavior Haag *et al.* (1995) observed in the lampsiline *Hamiota perovalis* (Conrad, 1834) which uses a superconglutinate lure. This behavior was most pronounced in *Tritogonia verrucosa* and *Quadrula fragosa*, species with the largest displays in our study, but was also noticeable in *Cyclonaias tuberculata* and to a lesser extent in *Q. pustulosa*. Presumably this behavior has evolved to attract nocturnally foraging ictalurids. In contrast, *Q. metanevra* remains mostly buried while displaying its diminutive, pale colored lure. Though small, this display is conspicuous and presumably resembles a small generic food item to sight-feeding minnows (Pflieger 1997). Remaining buried might improve the display's effectiveness by concealing the shell, a behavior we have also seen in *Lampsilis higginsii* (Lea, 1857), and to a lesser degree in *L. cardium* Rafinesque, 1820, which display a minnow-like lure to attract piscivorous hosts. The excurrent aperture of the closely related *Q. cylindrica* (also a member of the *metanevra* species group) is not inflated as in *Q. metanevra*, but is brightly-colored (Barnhart *et al.* 2008). These displays presumably elicit feeding encounters from foraging cyprinids, as do the small reddish or white conglutinates released by *Fusconaia* Simpson, 1900 and *Pleurobema* Rafinesque, 1819 (Tribe Pleurobemini) (Haag and Warren 2003).

Glochidia release behaviors

Quadruline unionids transfer glochidia from the marsupial demibranchs to the mantle magazine (Barnhart *et al.* 2008), a storage pocket formed by the swollen mantle (display) surrounding the excurrent aperture, where they are held before release. From the mantle magazine, transfer of glochidia to the host occurs by reflexive release (forceful expulsion of glochidia), extraction by the host, or conglutinate release (Barnhart *et al.* 2008).

Cyclonaias tuberculata is one of the few unionids that exhibit multiple host infection behaviors, in this case, a mantle display and amorphous conglutinate. This bimodal system is analogous to the lampsiline genus *Hamiota* Roe and Hartfield, 2005, where the female has both a mantle display and releases a superconglutinate (Hartfield and Butler 1997). *Cyclonaias tuberculata* gradually released gelatinous conglutinates with embedded glochidia, allowing them to trail behind the mussel and sway in the current, eventually detaching from the mussel, an effect also seen in *Hamiota* (Haag *et al.* 1995, Hartfield and Butler 1997). As with mantle displays, these conglutinates could function as a visual or chemical lure. Similar to *Hamiota*, we suspect the entire contents of the marsupia are released based on our observations, but this assumption needs to be examined further. In *Hamiota*, however, some individuals use both strategies at different times during the brooding period (Hartfield and Butler 1997). This is apparently not the case with *C. tuberculata* which likely use one method or the other, at least during a brooding period, because glochidia of displaying individuals were loosely assembled in the mantle magazine, whereas glochidia of conglutinate producers were embedded in a gelatinous mucous. Zanatta *et al.* (2007) discussed several hypotheses for the existence and maintenance of polymorphic lure morphologies in *Lampsilis fasciola* Rafinesque, 1820, which could also apply to the strategies seen in *C. tuberculata*.

Structured conglutinates are not used by quadrulines as primary host infection strategy as far as we know, although they are often released prematurely with eggs or undeveloped glochidia when disturbed (Lefevre and Curtis 1912). We have seen *Quadrula fragosa*, *Q. quadrula* (Rafinesque, 1820), and *Tritogonia verrucosa* release conglutinates with mature glochidia on occasion, with those of *T. verrucosa* being more fragile and easily fragmented. In contrast, several other amblemine genera have functionally structured conglutinates (Watters 2008) as their primary host infection strategy, but apparently do not use reflexive release. It is likely that physical or proximal contact with displays by foraging fish stimulates reflexive glochidia release. We recorded several instances of reflexive release among displaying *Q. metanevra* and *Q. pustulosa* in response to physical stimuli. Barnhart *et al.* (2008) reported reflexive release in *Q. pustulosa*, *Q. cylindrica*, and *Cyclonaias tuberculata*, although in our study we did not elicit a reflexive release from displaying *C. tuberculata*. The proportion of glochidia in a brood ejected during a release is unknown. Reflexive release of glochidia could potentially infest multiple fish during a single event, particularly *Q. metanevra* parasitizing schooling minnows. Vicentini (2005) reported a type of reflexive release behavior in *Unio crassus* Philipsson in Retzius, 1788 which spout a fine stream of water with glochidia into the air, evidently attracting fish to the splashing water.

In contrast, *Quadrula fragosa* and *Tritogonia verrucosa* apparently rely on host fish to extract glochidia when they attack the display (Barnhart *et al.* 2008), a strategy similar to some lampsilines (Haag and Warren 1999). In the laboratory or field, we occasionally observed *Q. fragosa* and *T. verrucosa* gradually release whole or broken conglutinates unsolicited, but not via reflexive release. These releases could be either incidental spillage from the mantle magazine or an alternative strategy to infest the host. Barnhart *et al.* (2008) postulated that species using both mantle lures and releasing conglutinates potentially could contact a wider range of hosts, and it is conceivable that catfish, perhaps smaller individuals, become infested by consuming these conglutinates.

Brooding characteristics described in this study represent a diverse set of morphological and behavioral adaptations to facilitate glochidia transfer to host fish, and exemplifies the diversity within the Quadrulini. Mantle display, conglutinate morphology, and glochidia release behaviors can be informative characters in phylogenetic studies (Zanatta and Murphy 2006, Watters 2008). While our results offer no conclusive insights into evolutionary relationships among quadruline species, because of, in part, insufficient species representation, the distribution of display and glochidia release character states corroborate aspects of quadruline phylogeny. For example, the similar display morphology of *Cyclonaias tuberculata* and *Quadrula pustulosa* support Campbell *et al.*'s (2005) placement of *Cyclonaias* within the Quadrulini and its apparent relationship with the *pustulosa* species group. Similarly, the relatively diminutive mantle displays, use of reflexive glochidia release, and unique host association with Cyprinidae corroborate the relatively close evolutionary relationship between *Q. metanevra* and *Q. cylindrica* (Serb *et al.* 2003).

As mantle display morphology and glochidia brooding and release behaviors are described for additional quadruline species, these character states, as well as glochidia morphology and host fish associations, will enhance our understanding of unionid reproductive biology and may help resolve questions of phylogeny and classification.

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